Common 3 and 10 Hz oscillations modulate human eye and finger movements while they simultaneously track a visual target

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1. A 10 Hz range centrally originating oscillation has been found to modulate slow finger movements and anticipatory smooth eye movements. To determine if an interaction or linkage occurs between these two central oscillations during combined visuo-manual tracking, frequency and coherence analysis were performed on finger and eye movements while they simultaneously tracked a visual target moving in intermittently visible sinusoidal patterns.
2. Two different frequencies of common or linked oscillation were found. The first, at 2–3 Hz, was dependent on visual feedback of target and finger tracking positions. The second, at around 10 Hz, still occurred when both target and finger positions were largely obscured, indicating that this common oscillation was generated internally by the motor system independent of visual feedback. Both 3 and 10 Hz oscillation frequencies were also shared by the right and left fingers if subjects used these together to track a visual target.
3. The linking of the 10 Hz range oscillations between the eyes and finger was task specific; it never occurred when eye and finger movements were made simultaneously and *independently*, but only when they moved simultaneously and followed the target *together*. However, although specific for tracking by the eyes and fingers together, the linking behaviour did not appear to be a prerequisite for such tracking, since significant coherence in the 10 Hz range was only present in a proportion of trials where these combined movements were made.
4. The experiments show that common oscillations may modulate anatomically very distinct structures, indicating that single central oscillations may have a widespread distribution in the central nervous system. The task-specific manifestation of the common oscillation in the eye and finger suggests that such mechanisms may have a functional role in hand–eye co-ordination.

The motor output from the central nervous system (CNS) is modulated by rhythmic activity at certain frequencies. Such rhythms have been demonstrated by direct recordings from the brain (Adrian & Moruzzi, 1939; Murthy & Fetz, 1992; Salmelin & Hari, 1994) and are manifest in distal limb and respiratory muscle activity (Elble & Randall, 1976; Kirkwood *et al.* 1982; Bruce & Goldman, 1983; Keidel *et al.* 1990; Farmer *et al.* 1993; Vallbo & Wessberg, 1993; Conway *et al.* 1995; McAuley *et al.* 1997). It has been suggested that these rhythmic modulations may be important in 'linking' related signals involved in motor control (Llinás, 1991; Welsh & Llinás, 1997). In other words, if neurones controlling the activity of certain muscles must act in concert to perform a desired task, they could be 'linked' together during the programming and execution of this task by superimposing a common rhythmic modulation upon their firing patterns.

To explore this possible role of rhythmic activity in the motor system, it is necessary to demonstrate (i) that different central or peripheral structures display the same centrally originating oscillation and (ii) that this sharing of oscillations is not fixed but occurs specifically when the structures act in concert during the performance of a certain motor task.

Direct central recordings in animals have revealed synchronized oscillatory activity in relation to sensorimotor tasks between neurones quite widely separated over the cortical surface (e.g. Murthy & Fetz, 1992; Nicolelis *et al.* 1995). This suggests that linking or sharing may occur between oscillations in cortical areas controlling different peripheral structures. Task specificity of such linking is suggested by the finding that cortical 25 Hz range oscillations in the monkey only become widespread during the performance of complex motor activity but remain localized if simple over-learnt movements are made (Murthy & Fetz, 1992). Welsh & Llinás (1997) have demonstrated that the pattern of synchronized units in the inferior olive of rats may be specific for certain phases of licking behaviour, although the 6 Hz frequency of this synchronized modulation is directly tied to the lick frequency, indicating that the pattern may merely reflect that different units fire at different phases of each lick.

Since central oscillations often become manifest as a modulation of electromyogram (EMG) activity or as tremor, a number of studies have looked at the oscillatory activity simultaneously present in different peripheral structures to see if they reflect a single common modulation. This indirect approach allows investigations to be conducted more easily in the human. However many human studies do not reveal linking between peripheral rhythms. The tremor oscillations in the left and right hands on posture appear to be independent (Marsden *et al.* 1969), as do the surface EMG oscillations in different simultaneously contracting hand muscles (McAuley & Brown, 1995), in left and right biceps while lifting a weight in both hands (Bruce & Ackerson, 1986) and in a variety of different proximal muscles analysed during postural activity (J. H. McAuley, T. C. Britton, J. C. Rothwell, L. J. Findley & C. D. Marsden, unpublished observations). In contrast, coherence analysis between single motor units of different small hand muscles contracting together reveals a common modulation at 16–32 Hz (Farmer *et al.* 1993) while multiunit EMG correlations in the monkey during the hold phase of pinch-grip tasks are coherent over a wide frequency range, with a peak coherence in the 20 Hz range (Baker *et al.* 1997).

Respiratory muscle EMG recordings provide a clear demonstration of linking between the oscillations of different peripheral structures (Bruce & Ackerson, 1986; Smith & Denny, 1990). This linking is again found to be task specific in that it occurs during breathing but not during non-respiratory activity such as speech.

The recent finding of 10 Hz range peripheral oscillations modulating smooth anticipatory eye movements (McAuley *et al.* 1999) provides an opportunity to look at linking between new and interesting combinations of peripheral structures. The present study investigates linking of oscillations modulating eye movements and finger movements while the eyes and finger simultaneously track the same visual target (visuo-manual tracking). Previous studies on slow finger movements have demonstrated a strong 10 Hz range oscillation (Vallbo & Wessberg, 1993; Wessberg & Vallbo, 1995); such oscillations are similar to the anticipatory smooth eye movement modulations in that they both originate centrally and both occur specifically when the structures move smoothly rather than when finger position is held at rest or when gaze is fixed.

Choosing to study oscillations in the eye and limb, as opposed to those in more similar structures, may give a clearer insight into the nature of central rhythms and their role in motor control.

First, since the eyes and limb are such anatomically distinct structures, any linking which is found is likely to originate at a high level in the CNS where it may be functionally important in motor processing. Studies on more closely related structures may reveal a linking which is merely due to modulation by EMG cross-talk, by shared mechanically transmitted tremor, by shared peripheral feedback reflex loops or by inputs from branches of shared corticospinal axons.

Second, previous work on visuo-manual tracking has already demonstrated a rich and high level interaction between the two motor systems. For example, attempting to make smooth eye movements in the dark with the aid of a retinal after-image of the hand is easier if the subject actually moves his unseen hand in the same pattern (Jordan, 1970). This interaction seems to occur at the level of motor programming because the improvement is greater for active than for passive hand movements. The tremulous oscillations superimposed upon limb activity may themselves be influenced by visual information. The hand tremor spectral peak at around 9 Hz can disappear on removing visual feedback and its frequency can be shifted by introducing extra artificial visual feedback delays (Sutton & Sykes, 1967; Merton *et al.* 1967). The frequencies of tremor during visually guided fine finger movements have also been shown to depend upon the complexity of the task (van Galen *et al.* 1990). Since oscillations at around 10 Hz modulate eye movements as well as finger movements, visuo-manual tracking would be an excellent protocol for the investigation of task-specific linking and other interactions between central rhythms manifest in different peripheral structures.

In the present study, subjects' eye and finger movements are measured as they track sinusoidally moving visual targets. Coherence analysis between these signals demonstrates that linking of eye and limb oscillations does indeed occur. The linking appears to be task specific since it is never present when the eyes and finger move independently but only when they move together as part of a combined tracking strategy involving hand–eye co-ordination.

METHODS

The experiments were performed on 14 normal subjects (10 male, 4 female) whose ages ranged from 18 to 41. All subjects had adequate visual acuity for viewing the targets, either normally or by correction with contact lenses. Informed consent was obtained from each subject and the study was performed according to the Declaration of Helsinki with local ethical committee approval.

Equipment and set-up

Eye and finger movements were studied while subjects attempted to track horizontal sinusoidally moving visual targets simultaneously with the eyes and the right index finger or both index fingers, sometimes with a concurrent visual display of finger position.

Each subject was seated comfortably in a totally dark area facing a large computer monitor screen. A target on the screen consisting of a small red cross on a black background could be made to move in smooth horizontal sinusoidal patterns of varying frequency and amplitude and to disappear and reappear at different points in its cycle. In addition to the +-shaped cross of the target, a similar ×-shaped cross moving horizontally just below the target cross could display finger position either continuously or intermittently. The software also enabled the target's position to be recorded on-line for subsequent data analysis.

Movements of the left eye were recorded by infrared reflection spectacles (Microguide Series 1000, Dolton, IL, USA). The DC output from the recording spectacles was amplified and first-order low-pass filtered by −3 dB at 100 Hz (Microguide Series 5000 amplifier) to give an eye position signal. This signal was also analog differentiated to give eye velocity. A bitebar assembly fixed the head in a stationary position and the infrared recording spectacles were firmly fixed around the forehead. A lightweight piezo-resistive accelerometer (Vibro-Meter SA105) attached to the frame of the spectacles recorded any residual movements of the head or spectacles. The DC accelerometer head signal was amplified and first-order high-pass filtered by −3 dB with a time constant of 300 ms.

For measuring finger movements, the right forearm was held in a semi-pronated position in a rigid moulded foam-covered support. The subject moved his outstretched right index finger in the horizontal plane in a flexing-extending direction about the metacarpophalangeal (MCP) joint. The interphalangeal joints of the finger were kept extended. The remaining fingers of the hand were positioned comfortably so that they did not touch or otherwise interfere with movements of the index finger. A lightweight (5 g for the finger attachment end) goniometer (Penny & Giles-XM110, Newport, UK) was attached at one end to the distal phalanges of the index finger and at the other to the back of the hand. The goniometer recorded the angle between these two fixation points (i.e. MCP joint angle) without significantly resisting or restricting movements about the MCP joint.

The eye position, finger position and target position signals were on-line analog-differentiated to give velocity signals. The original position signals and derived velocity signals, together with the head accelerometer signal, were all digitally sampled at 500 Hz with 12-bit resolution by a 1401-plus analog-to-digital converter (CED, Cambridge, UK). The data were displayed and stored on computer disk by a software package (CED-Spike 2) running on a PC.

Before each set of trial parameters, eye movements were calibrated so that approximately linear amplification was achieved for eye movements in either direction about central fixation. Finger movements were calibrated so that the finger position corresponding to extreme right target position was at full, but not forced, MCP joint extension and left target position was at about 45 deg joint flexion.

In some experiments, tracking of visual targets was performed with both right and left index fingers together. (The two fingers were moved in the same direction so that right finger extension and left finger flexion corresponded to target motion to the right and vice versa for target motion to the left.) Recordings of the positions and velocities of the two fingers were made simultaneously with two similar goniometers. When a visual display of finger position was provided, only the position of the right finger was shown.

Data analysis

Analysis of the eye and finger movement data was performed off-line in the time and frequency domains by programs running in the CED Spike 2 environment.

For analysis of the tremor of smooth eye movements, saccades were removed from the eye velocity traces (Fig. 2) after identification of their start and end points. The saccades were replaced by straight lines joining these start and end-points. Each 1024 point block of data (2 s) was normalized to remove DC offset before spectral analysis.

Power spectra were calculated from these modified data blocks and thus represented frequencies of activity due to non-saccadic tremulous oscillations of the eye together with residual components of smooth tracking at the target frequency. The power spectra had frequency bins of approximately 0·5 Hz width with the highest frequency bin at the Nyquist frequency of 250 Hz. Similar power spectra were derived from the raw finger velocity records and from head tremor accelerometer records. Averaged power spectra were then obtained over around 80 fast Fourier transform (FFT) data blocks. The program also allowed viewing of running averages arising from the accumulation of successive contiguous data blocks up to the maximum of 80 blocks (a full 20-run trial). Confidence intervals (95%) were also calculated at each frequency bin for these 80-block mean values. A peak was said to exist in an averaged spectrum if there existed a region of elevated power in the 3 or 10 Hz range that was greater than surrounding power by at least the 95% confidence interval for the mean spectral power at that frequency.

To investigate linking between smooth eye movement oscillations and finger oscillations, the coherence between the smooth eye velocity records and the corresponding finger velocity records over successive contiguous paired data blocks was calculated (Jenkins & Watts, 1968):

$$\text{Coherence} = \frac{|\Sigma\,\text{CSD}|^2}{\Sigma\,\text{PSD}_a \times \Sigma\,\text{PSD}_b},$$

where CSD is the cross-spectral density for each block and PSD is the power spectral density for the two signals.

Any frequency components common to the two records would thus show up as significant coherence. Phase plots determined the relative timing of common oscillations; for the summed value of CSDs over a number of blocks, the phase angle difference is the arctangent of the ratio of the imaginary and real components. Phase determination at a certain frequency is only relevant if there is significant coherence at that frequency.

Protocol

In each trial, the target moved in a horizontal sinusoidal pattern of frequency 0·25 or 0·375 Hz and amplitude 20 deg visual arc. Preliminary experiments had determined that these parameters were suitable for generating 10 Hz range oscillations superimposed upon both the eye and finger tracking movements. After a short period of practising smooth sinusoidal finger movements guided by the visual display of finger position, in each of four experimental sessions subjects tracked at least 25 runs of target sinusoidal motion under one of four different conditions described below. Each run started from the right side of the screen and continued for 8 s. After a few seconds rest, subjects triggered the onset of the next run themselves. The last 20 contiguous runs (80 FFT blocks of 2 s duration) were analysed and constituted a single 'trial'.

The four experimental sessions were conducted under different conditions in the following sequence.

Condition 1. Both the target and finger display positions were continuously visible. Subjects were asked to track smoothly, fixing their gaze on the target and following in the same pattern with the finger. They were told that it was more important to move the finger smoothly than to attempt to keep the finger position marker exactly aligned with the target position marker. Likewise, it was requested that concentration of gaze be kept on the target and only 'peripheral vision' be used to guide the finger instead of making continual shifts of gaze to the finger position marker. All subjects felt they could comply comfortably with these requests within the first five trial sections.

Condition 2. The target position was continuously visible but the finger following position was invisible during those time periods corresponding to the central 75% of each target sinusoid sweep. This corresponded to the central 92·4% of amplitude displacement. Thus, subjects could use direct visual information at the left and right extremes of target motion to maintain the correct overall amplitude, frequency and phase of finger following but the bulk of finger motion was now without visual feedback.

Condition 3. Both the finger and the target positions disappeared for 75% of each sweep time, again during the period corresponding to the central part of the target sinusoid pattern, while eye and finger tracking continued as smoothly as possible. Subjects now had to perform anticipatory eye movements during the bulk of target motion as well as finger movements without visual feedback.

Condition 4. To investigate eye and finger movements made independently rather than while tracking the same target, subjects tracked the same target pattern as in condition 2 but were now instructed to move the finger at random while tracking the target with the eyes only. Subjects attempted to make finger movements of a similar general speed to that of previous trials.

Finally, to see if there was linking between finger oscillations on the right and left sides of the body, the experiments were repeated in some subjects while tracking with both right and left index fingers together.

RESULTS

All subjects could perform the tracking tasks with reasonable success under all four conditions, namely (i) target and finger following completely visible, (ii) target completely visible and finger following only intermittently visible at the edges of the waveform, (iii) both target and finger following only intermittently visible and (iv) finger position intermittently visible but with the finger moving randomly instead of tracking the target (Fig. 1). Subjects generally found the fourth task hardest to perform. Anticipatory eye movement tracking in the absence of a visual target was subjectively no more difficult, and sometimes easier, when tracking simultaneously with the finger than when moving the eyes alone (cf. Jordan, 1970). It was generally too difficult to perform anticipatory eye movements when simultaneously moving the finger randomly so the target was made continuously visible in condition 4.

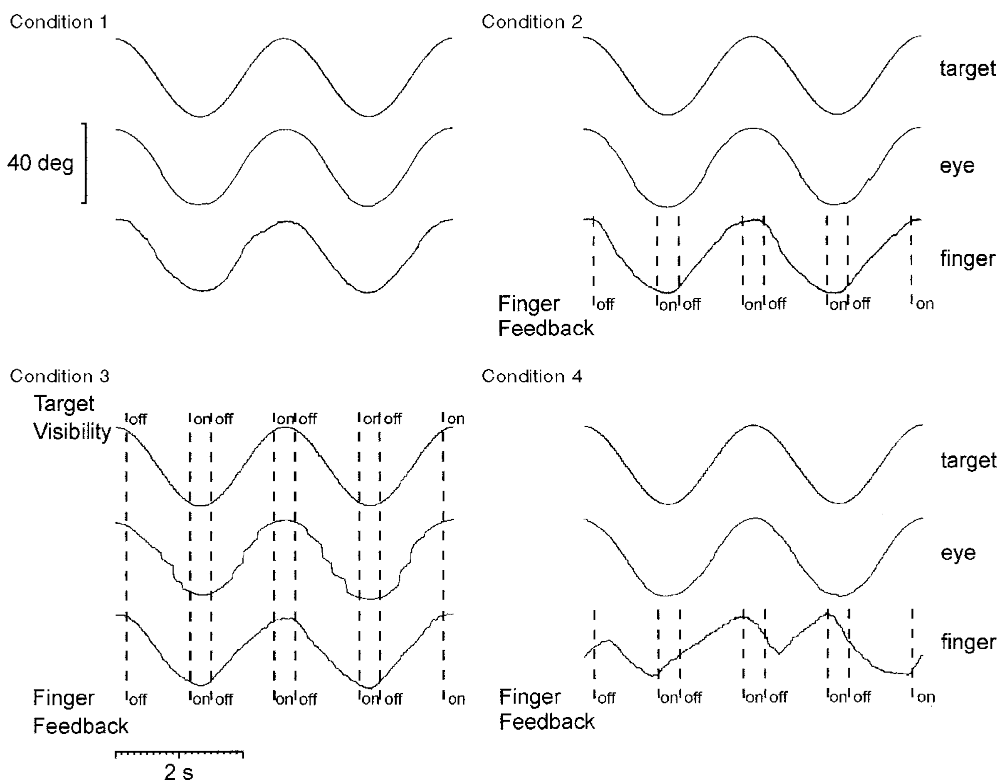

Figure 1. Eye and finger tracking under different feedback conditions

Sinusoidal tracking by the eyes and finger in subject M.R. The target and finger positions are displayed to the subject. The figure shows target position, eye position and finger position, together with periods where the finger following or target position is obscured. Four different conditions are studied: condition 1, target and finger following always visible; condition 2, finger following only visible at extremes; condition 3, both finger and target only visible at extremes; condition 4, finger following only visible at extremes and random instead of tracking finger movements.

Table 1. Peaks in eye and finger velocity spectra

	10 Hz range peaks				3 Hz range peaks			
	Condition 1	Condition 2	Condition 3	Condition 4	Condition 1	Condition 2	Condition 3	Condition 4
Eye peaks								
No.	10	8	7	7	4	0	0	0
Frequency (Hz)	$9{\cdot}0 \pm 1{\cdot}0$	$8{\cdot}6 \pm 0{\cdot}95$	$7{\cdot}9 \pm 0{\cdot}53$	$9{\cdot}0 \pm 1{\cdot}04$	$2{\cdot}9 \pm 0{\cdot}25$	—	—	—
Finger Peaks								
No.	13	13	12	11	0	0	0	0
Frequency (Hz)	$8{\cdot}4 \pm 0{\cdot}9$	$8{\cdot}2 \pm 0{\cdot}52$	$8{\cdot}4 \pm 0{\cdot}7$	$8{\cdot}1 \pm 0{\cdot}58$	—	—	—	—
Coherence								
No.	5	8	8	0	14	3	1	1
Frequency (Hz)	$8{\cdot}6 \pm 0{\cdot}4$	$8{\cdot}1 \pm 0{\cdot}82$	$8{\cdot}3 \pm 0{\cdot}46$	—	$2{\cdot}5 \pm 0{\cdot}31$	$2{\cdot}7 \pm 0{\cdot}29$	2·5	3·0
Time lag (ms)	-50 ± 27	-59 ± 17	-19 ± 43	—	-7 ± 51	-20 ± 57	−60	50

Number of subjects out of 14 showing distinguishable peaks in eye velocity and finger velocity spectra (averaged over 80 FFT blocks) in the 10 and 3 Hz ranges under the four conditions. Also indicated are the number of coherence spectra with a significant peak (defined as two contiguous frequency bins above the 95% confidence line occurring within 1 Hz of a power spectral peak). Below each number is shown mean values (Hz) and standard deviations (S.D.) of all peaks and estimates of coherence time lags (ms) estimated from phase plots.

Finger oscillations

All but one subject consistently showed oscillations of finger movement that were easily apparent in the finger velocity traces (Fig. 2). The oscillation period was generally around 120 ms and its peak-to-peak amplitude was of the order of 10–40 deg s^{-1}, much greater than the tremor if the finger was simply held stationary against gravity. The finger oscillation was considered to be the same phenomenon as that initially described by Vallbo & Wessberg (1993). Recordings under all four trial conditions showed these oscillations. During trials where visual feedback of finger position was present (condition 1), slower fluctuations of period around 300–400 ms were also sometimes discerned.

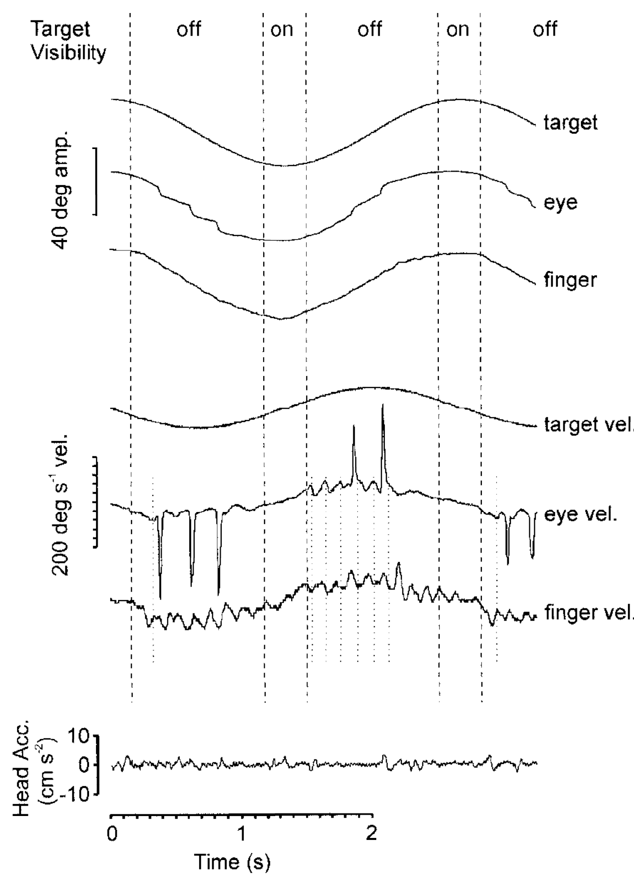

Figure 2. Eye and finger tracking of intermittently obscured target (condition 3)

Position and velocity (vel.) traces of eye and finger tracking by subject M.M. when the finger following and target are intermittently obscured. Modulations of period around 120 ms are visible in both the eye and finger velocity traces. Large spikes in the eye velocity trace correspond to saccades made when the target is not visible. A constant phase relationship between the two modulations is suggested by the dotted vertical lines aligned with the eye modulation peaks; each finger peak leads the corresponding eye peak by roughly 40–50 ms. There are no such modulations in the corresponding head acceleration record.

Power spectral estimates of finger velocity traces averaged over each trial revealed a spectral peak at around 8 Hz (Figs 3*B*, 4*B*, 5*A* and 6*A*) corresponding to the finger oscillations seen in the time domain. The mean values (± S.D.) of these peaks are shown in Table 1. (Only one subject did not display an easily distinguished spectral peak in this range.) High spectral power was also present at very low frequencies due to tracking at the target sinusoid frequency. The 300–400 ms range periodicity was never strong enough to manifest as a separate 3 Hz range spectral peak.

Eye oscillations

The eye velocity records sometimes revealed oscillations of period around 80–120 ms (Fig. 2). These oscillations were of greater amplitude (up to 15 deg s^{-1}) during anticipatory smooth eye movement tracking than when the target was continuously visible. They sometimes occurred concurrently with finger movement oscillations of a similar period (Fig. 2).

Power spectral analysis of saccade-removed eye velocity traces sometimes revealed broad spectral peaks with central frequency values around 8–9 Hz (Figs 3*A* and 4*A*). There were also sometimes spectral peaks in a 2–3 Hz range. These peaks were not simply artefacts generated by the procedure that removed the saccades from the eye velocity traces (McAuley *et al.* 1999). As for the finger spectra, high power was also present at very low frequencies.

The number of subjects out of 14 whose spectra showed an easily distinguishable peak in these two ranges for each condition are shown in Table 1, together with the peaks' mean frequency values. The incidence of clear spectral 10 Hz range peaks in condition 3 (where the central 92·4% of the smoothly moving target was obscured) was little different from that in conditions 1 and 2 (target continuously visible), despite the fact that 10 Hz oscillations are mainly a feature of smooth *anticipatory* eye movements (McAuley *et al.* 1999). This is because only half the subjects could make smooth anticipatory eye movements; the 10 Hz modulations can sometimes appear during continuous feedback tracking but *never when the eyes do not move smoothly*. In condition 3, the subjects who did not make smooth anticipatory movements instead tracked the obscured sinusoid by a series of staggered saccades with intervening stationary periods. When a 10 Hz range peak was present in condition 3 (i.e. in those subjects able to make smooth anticipatory movements), the power of the 10 Hz modulation was considerably greater than that during smooth tracking with visual feedback, perhaps because the anticipatory movements were not 'locked' onto the target by velocity error feedback.

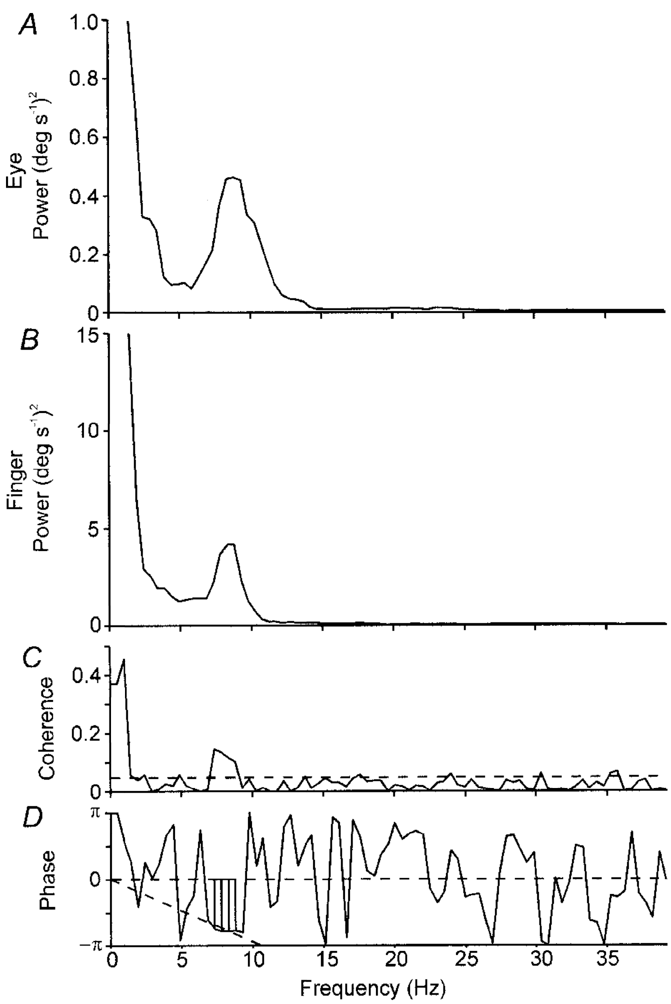

Figure 3. Spectra of eye and finger tracking of intermittently obscured target (condition 3)

Power spectra averaged over 80 data blocks of saccade-removed eye velocity (*A*), finger velocity (*B*) and their coherence (*C*) and phase relationship (*D*) during tracking by subject M.M. The data include the brief sections seen in Fig. 2. The horizontal line on the coherence plot indicates the 95% confidence threshold line for non-zero coherence for that 80-block trial. There is thus significant coherence between the peak frequency of modulation at 8 Hz in the two spectra. (In fact, the *P* value for this peak is as little as $2{\cdot}7 \times 10^{-6}$.) The dashed sloping line in *D* is drawn by eye from the origin to fit the phase values within the range of significant coherence. (Phase values at non-coherent frequencies are meaningless; those at significantly coherent frequencies are highlighted with vertical lines.) The slope of the line gives an estimate of time lag of 48 ms of the eyes behind the finger (time lag = slope/2π). There is also significant coherence at very low frequencies because the eyes and finger are tracking the same slow target movement. These low frequency tracking oscillations are exactly out of phase in this spectrum because the analysis technique subtracts a scaled target velocity trace from the eye movement velocity trace to aid in identification and removal of saccades and the scaled target amplitude was here slightly too large.

Occasionally, an eye velocity peak was present at around 16 Hz; this corresponded to eye oscillations seen at that frequency in the raw records. Possibly the eyes were now being modulated at a harmonic of the 8 Hz frequency. Such peaks were not included in averages of the eye oscillation peak values.

Coherence between finger and eye movement oscillations

Coherence analysis between corresponding finger velocity and eye velocity spectra sometimes revealed a significant level of coherence in the frequency range of the two oscillations. This indicated that a single oscillation was sometimes common to the two motor systems. Significant coherence (here defined as at least two contiguous bins above the 95% confidence threshold line for non-zero coherence) in a range around 8–10 Hz was sometimes present in conditions 1, 2 and 3 but never in condition 4 (Table 1). Condition 2 was different from condition 4 only in respect of the finger moving with the eyes and target instead of randomly, but 8 out of 14 subjects showed 10 Hz range coherence in condition 2. On a χ^2 test (Microsoft Excel) this was significantly different ($P = 0{\cdot}0008$) from the zero incidence of coherence in condition 4. This indicated that linkage between the oscillations was specific to tasks where the movements themselves were linked together in tracking the same visual target.

The presence of coherence was generally dependent on the presence of peaks in the two power spectra; the subject who never had a finger 10 Hz range peak also never showed any coherence. The inconsistent coherence was thus partly due to the inconsistent presence of clear 10 Hz range eye oscillations described above. The uniform absence of coherence in condition 4 occurred *despite the fact that peaks were still often present in the individual eye and finger power spectra.*

Examination of the eye and finger position records did not reveal any correlation between the quality or similarity of their tracking and the presence of coherent oscillations.

The phase plots, which show the value of the phase difference between any common coherent oscillations, revealed a variable phase relationship from trial to trial (Table 1), indicating that in different 80-block trials there was a different fixed time lag between finger oscillations and eye oscillations. The variability was indicated by the wide standard deviations of the time lag values. (The phase was clearly relatively fixed *within* 80-block trials because this is a prerequisite for significant coherence.)

It became apparent during coherence analysis that certain periods within some trials exhibited quite strong coherence whereas others contained no coherence. This often served to reduce greatly the overall coherence for the 80 blocks of a full session, sometimes to below the 95% confidence level.

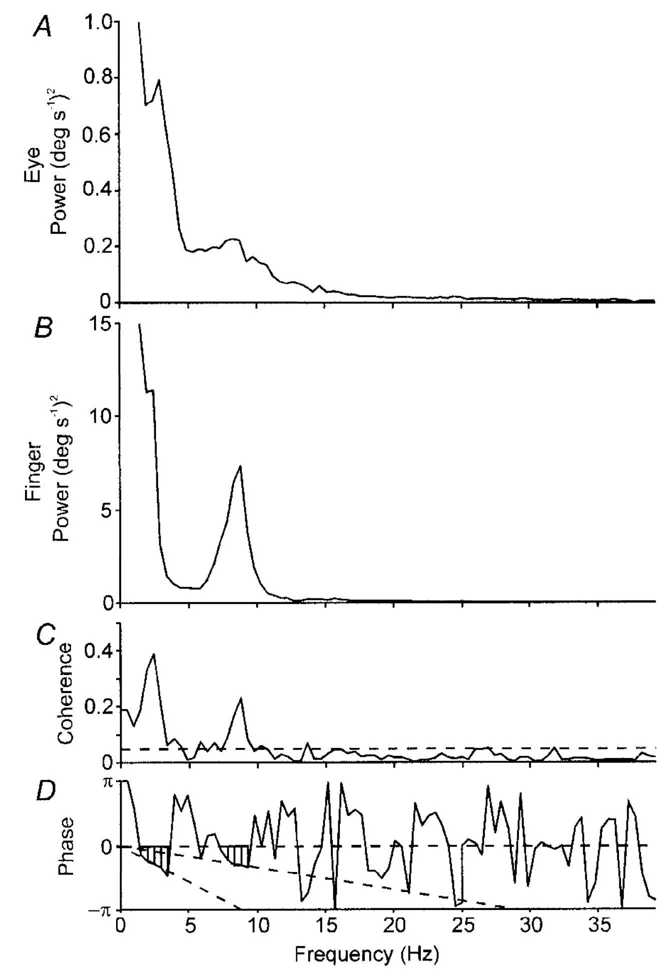

Figure 4. Spectra of eye and finger tracking with visual feedback (condition 1)

Power spectra averaged over 80 blocks of saccade-removed eye velocity (*A*), finger velocity (*B*) and their coherence (*C*) and phase relationship (*D*) during tracking by subject M.M. when both finger following and target are always visible (condition 1). There is significant coherence between the peak frequencies of modulation at 8 Hz in the two spectra ($P = 1{\cdot}1 \times 10^{-9}$) with a lag of 18 ms of the eyes behind the finger. There is now also significant coherence at a separate lower frequency of 2·5 Hz ($P = 1{\cdot}1 \times 10^{-19}$) with a different time lag of 65 ms of eyes behind finger.

In addition, if two different data periods of around 20–40 contiguous blocks were analysed separately, they might each individually show clear coherence, but when combined the coherences cancelled out. This was seen to be due to a different phase relationship of eye and finger oscillation between the two periods. These observations were difficult to quantify because of the progressively lower level of accuracy in determining coherence for data sections shorter than around 40 blocks. Nevertheless, the observations suggested that coherence between the oscillations could fluctuate in strength over periods of around 1–3 min within a trial and that the phase relationship of the coherence could also vary over similar periods.

Note that for waveform signals, coherence is dependent not only upon a similar frequency and phase relationship of the two oscillations, but also upon a constant ratio of amplitudes of the oscillation in the two signals. Thus, if the strength of manifestation of a central oscillation was able to vary independently between the eyes and finger, the observed coherence level would be considerably lowered. The fluctuations in coherence level in these experiments might be partly due to the observed variability in the strength of 10 Hz range eye oscillation that appeared to be both independent of and greater in magnitude than the variability of finger oscillation amplitude. (Eye velocity spectral peaks were also generally broader than those of finger velocity.)

Significant coherence was never present for periods *within* sessions when the finger moved independently of the eyes (condition 4).

3 Hz Oscillations

As mentioned above, in trials where visual feedback of limb position was provided and the target was fully visible (condition 1), there were sometimes clear peaks in the eye movement power spectra at a separate frequency around 2–3 Hz (Table 1). No clear peaks were present in the corresponding finger spectra, although there was sometimes a small 'shoulder' in the spectrum at this frequency. This oscillation has previously been shown to occur during smooth visually guided eye movements without finger movement (Robinson *et al.* 1986). It is unclear why they were not strongly enough manifest to be visible in the eye spectra in conditions 2 and 4, when feedback-guided eye movements were made simultaneously with *non*-feedback-guided finger movements.

The coherence spectra of condition 1 had clearly distinguished significant coherence in a peak at around 2–3 Hz in *all* subjects (Table 1), in addition to that previously described in the 10 Hz range. The consistent coherence (which indicates common oscillations independent of absolute amplitude) suggested that the oscillation was present in all of the eye and finger records but was not of great enough amplitude to give a clear peak above background power in all of the eye spectra or in any of the finger spectra. There was also occasionally coherence at 3 Hz in the other conditions. Possibly this related to imperceptible positional correction movements of eye and finger occurring during the relatively stationary periods at the edges of the sinusoid pattern when both eye and finger position were visible in all conditions. (Such a mechanism is not relevant

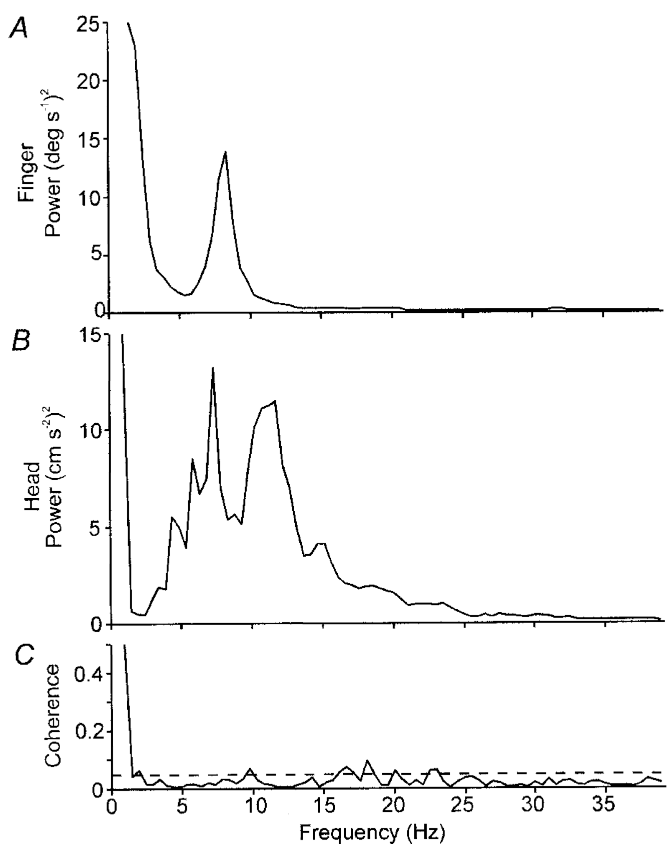

Figure 5. Spectra of finger tracking and head tremor (condition 3)

Averaged power spectra of 80 blocks of finger velocity (*A*), head tremor recorded by an accelerometer (*B*) and their coherence during a trial (condition 3) where there were marked peaks in both eye and head spectra (subject C.I.). There is no significant coherence between the two spectra at the frequency of the 8 Hz finger tremor peak. The finger oscillation thus does not spread to the head, thereby eliminating the possibility of common contamination of the eye and finger recordings via head tremor. Significant very low frequency coherence may relate to small tracking head movements at the 0·25 Hz target frequency.

for 10 Hz range oscillations because modulations at this frequency were specific for fast movements and so never occurred during these relatively stationary periods.) The uniform level of occurrence in the 14 subjects in condition 1 was nevertheless significantly different from that in the other conditions (χ^2 test of independence, $P = 4{\cdot}2 \times 10^{-8}$).

The 3 Hz range peak was a separate frequency of coherent oscillation rather than simply being harmonically related to the 10 Hz peak because (i) it was often of a frequency that was clearly not an arithmetic submultiple of the higher frequency peak, (ii) unlike the higher frequency peak, it occurred much less in spectra of trials where there was no continuous visual feedback of finger position and (iii) when 3 and 10 Hz coherence were simultaneously present, their phases were different (Fig. 4 and Table 1). The low frequency coherence therefore represented an independent process that was related to visual feedback.

Head accelerometer recordings

The possibility that the coherence between the eyes and finger was due to mechanical cross-contamination between the two structures was considered to be unlikely because of their wide anatomical separation and the effort made to fix the head and the hand. It was shown previously (McAuley *et al.* 1999) that a 10 Hz head tremor did not account for the eye oscillations either by movement of the infrared recording apparatus or via a vestibular reflex mechanism. In the present experiments, there was never any coherence between head tremor, as recorded by the accelerometer, and the finger oscillations (Fig. 5).

Coherence between right and left fingers

It has been shown that the 10 Hz range eye oscillation is consistently shared by both eyes with a zero phase lag between the eyes, suggesting that a single central oscillation drives the eyes in a binocular manner (McAuley *et al.* 1999). Such a central oscillation able to influence both eyes together, and also influence the finger when it moves in conjunction with the eyes, might be expected also to influence both right and left fingers if they performed the same tracking task. This was tested by repeating the experiment four times under conditions 1 and 2 while tracking with both index fingers simultaneously. Target movement to the right corresponded to an extension of the right finger and a flexion of the left finger while movement to the left was tracked by finger movements in the opposite directions. It was found that coherence existed between the 10 Hz range power spectra of the velocity traces of the two fingers (Fig. 6). This coherence was perhaps surprisingly weak, being of the same order of magnitude as that between finger and eye, and was not present at all in one of the records, where the peaks in the two power spectra were at clearly different frequencies separated by about 1·5 Hz. In the records showing coherence, the phase relation between the two fingers was not zero and was variable. The inconsistent coherence and non-zero variable phase indicated that, in contrast to the two eyes, the common central oscillation of finger movements was not mediated via a simple ‘hard-wired’ bimanual pathway, but was more akin to the ‘partial’ linking displayed between eye and finger oscillations. When visual feedback of the right finger position was continuously

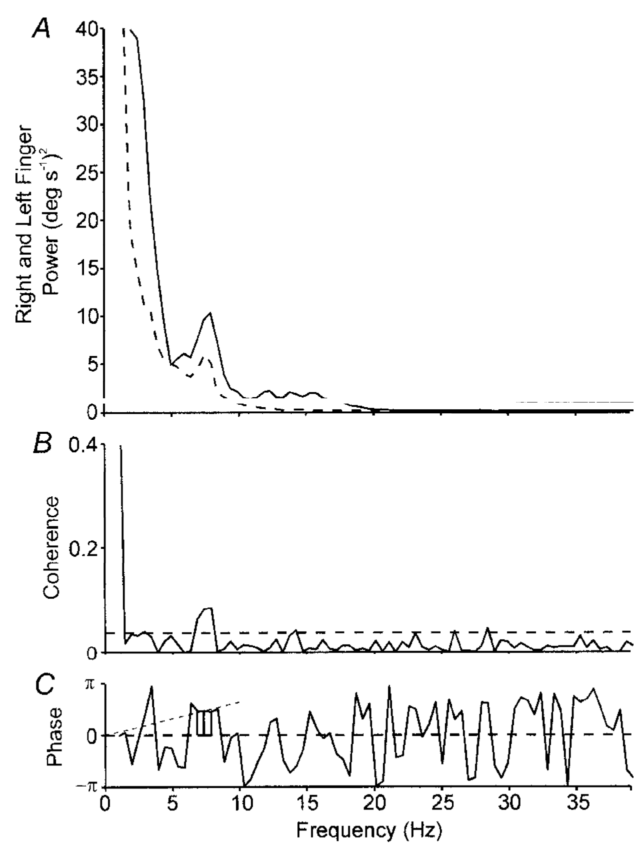

Figure 6. Spectra of right and left finger tracking with obscured visual feedback of finger position (condition 2)

Averaged power spectra of 80 blocks of right (continuous line) and left (dashed line) finger velocities (*A*) while both fingers track the target together (subject J.M.). Only the right finger following is displayed to the subject. The right finger following is intermittently obscured (like condition 2). The significant coherence ($P = 9{\cdot}0 \times 10^{-4}$) (*B*) indicates that the same oscillation is manifest bilaterally but the non-zero phase difference (*C*) reflects that this is not due to simple divergence of similar pathways.

available (condition 1), there was also modest coherence at the lower *circa* 3 Hz frequency (Fig. 7).

DISCUSSION

3 Hz range oscillations

A 3 Hz range modulation of smooth tracking eye movements has already been described (Robinson *et al.* 1986) and is thought to relate to visual feedback loop times or to the internal efference copy feedback loop time for prediction-boosted eye movement velocities (Barnes & Asselman, 1991). In those experiments the eyes tracked targets without additional tracking by other body parts. However, other studies have revealed that visually guided limb movements also exhibit a 2–3 Hz rhythmicity (Craik, 1947; Navas & Stark, 1968), although in humans this generally only occurs when the target moves unpredictably. Such target patterns are thought to be tracked by discrete limb movements generated by intermittent visual feedback occurring at this frequency so that movements are only made when the result of the previous movement has had time to be assessed (Miall *et al.* 1985).

It is therefore not surprising that in the present study, where both eye and finger tracking are simultaneously recorded, there is a 3 Hz range coherence between the two motor systems. The dependence on visual feedback that was suggested by previous studies is clearly illustrated by the presence of coherence in all subjects when both target and finger following are continuously visible (condition 1), but only rarely when either is partially absent. The occasionally significant coherence in the other trials is explainable by tracking at the still-visible edges of the sinusoid. The findings also illustrate that coherence analysis is a sensitive indicator of common oscillations because of its lack of dependence upon noise that is uncorrelated between the two signals; power spectral eye peaks were only visible in a proportion of records when the target was always visible and were never strong enough to be distinguishable as a separate peak in the other trial conditions. The universal coherence between condition 1 eye recordings and the corresponding finger recordings indicates that 2–3 Hz modulations of limb movement occur while tracking predictable as well as unpredictable targets and suggests that they are not manifest in finger power spectra (or in previous studies on limb oscillations) because of their small amplitude.

10 Hz range oscillations

Recent studies have demonstrated the presence of 10 Hz range oscillations during anticipatory smooth movements of the eyes (McAuley *et al.* 1999) and during smooth slow finger movements (Vallbo & Wessberg, 1993). This study shows that coherence sometimes exists between the 10 Hz range oscillations of these two structures. It is easy to exclude contaminating signals such as spreading mechanical oscillations as an explanation for the coherence because there is considerable anatomical separation and a lack of similarity between the eye and finger. In addition, the presence of common oscillations without a visual target means that the coherence cannot be due to shared peripheral

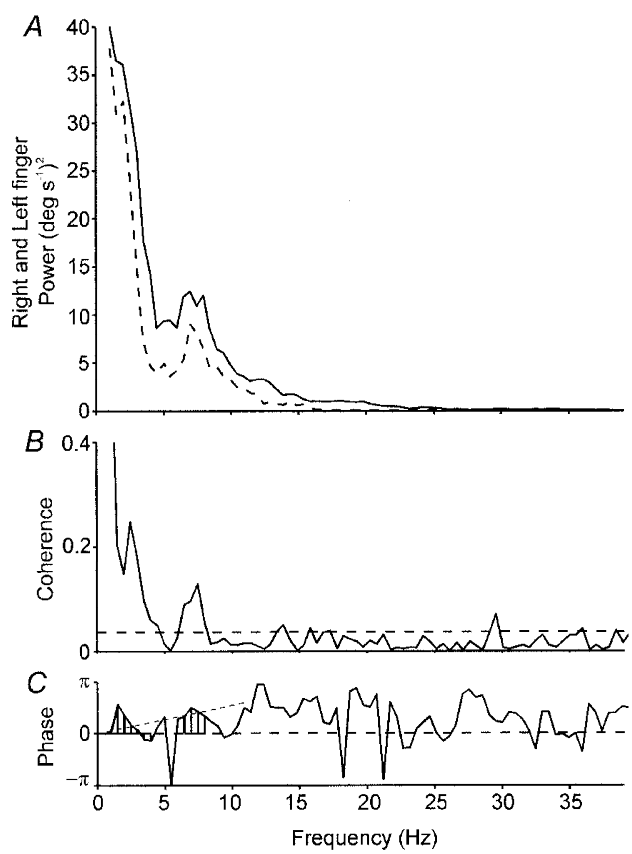

Figure 7. Spectra of right and left finger tracking with visual feedback of finger position (condition 1)

Averaged power spectra of 80 blocks of right (continuous line) and left (dashed line) finger velocities (*A*) while both fingers track the target together (subject J.M.). The right finger is now continuously visible (like condition 1). There is again a significant peak of coherence at 7–8 Hz ($P = 2{\cdot}0 \times 10^{-5}$) and probably also a 2·5 Hz range peak that appears distinct from the low frequency coherence occurring due to tracking of the same target. The phase of the 2·5 Hz coherence is difficult to interpret because of close association with target tracking coherence.

feedback loop resonances. It therefore seems that the structures may share a common CNS rhythmicity somewhere in the motor pathway. Previous animal studies directly recording cortical activity have shown a fairly widespread task-specific synchrony of central oscillations over the monkey pre-central gyrus (Murthy & Fetz, 1992) but these oscillations were in the 25 Hz range. Human magnetoencephalography (MEG) recordings during steady contraction have similarly revealed 20 Hz range coherence with finger muscle EMG oscillations; during *movement*, the coherence between different finger muscles shifts to the 10 Hz range, although the latter oscillation is not reflected in the MEG (Farmer, 1998). Welsh & Llinás (1995) have shown synchronized 6–10 Hz range oscillations between units within the inferior olive in a pattern dependent upon the phase of a repetitive movement. Since the cerebellum is closely associated with the control of smooth pursuit eye movements as well as smooth finger tracking, it is tempting to suggest that the same olivo-cerebellar synchronizing process could be the basis of the shared oscillations of the present study.

As in some previous studies (Murthy & Fetz, 1992; Welsh & Llinás, 1997; Baker *et al.* 1997), the common central rhythmicity appears to be *task specific*; the oscillations may become shared when the eyes and finger move together to track the same target but never when the finger is moved in an independent pattern. In the latter situation, the oscillations always run independently when they occur. The presence of task specificity suggests the existence of a functional role for such oscillators. Unlike the 3 Hz range oscillations, their presence and coherence is not dependent upon visual feedback and so this role might relate to the internal generation of co-ordinated motor activity. On the other hand, neither the coherent oscillations nor even independent eye or finger oscillations are universally present and are not found to be necessary for successful tracking of the target. Possibly a single oscillatory generator of the two smooth movements is only one of a number of strategies for performing such tasks or perhaps the variability in manifestation within a single task simply reflects that the central oscillations are not reliably recorded in the periphery.

Variability of coherence and phase relationships

The 3 Hz range oscillations in the eyes and finger would appear to be consistently linked in timing via common visual feedback. However, the varying phase relationship from trial to trial and between subjects indicates that the dependence on feedback is rather complex and not explainable in terms of delays for signal transmission along fixed afferent and efferent pathways.

The 10 Hz range coherent oscillations are variable in both their occurrence and in their phase relationship, again arguing against an explanation based upon branched hard-wired pathways. Even the linking of the 10 Hz range oscillation between the right and left fingers (also described by Wessberg, 1996) is here found to lack consistency and has a clearly non-zero phase relation. This plasticity of linking (especially that which is task specific) in some ways makes the oscillations more interesting to investigate as a potential mechanism of motor control.

A number of factors may together account for the observed variability.

(1) Measurement of eye velocity tremor and finger acceleration tremor are necessarily very indirect ways to record the behaviour of central oscillations. Independent variations in the strength of peripheral transmission of the linked central oscillation to the eyes and finger will degrade coherence because, although not dependent on the absolute amplitudes of the two signals, the estimate of coherence still depends upon a constant relative amplitude.

(2) A similar degradation of coherence arises from variability in the central origin of the component oscillations. The 10 Hz range eye movement oscillation is often not manifest at all. It is found to be strongest when making high velocity anticipatory smooth eye movements (above around 15 deg s^{-1}) but only some subjects can make such movements to a significant extent. Although made by a greater number of subjects, the oscillations occurring on tracking continuously visible sinusoids (conditions 1 and 2) are of lower amplitude. The frequency of 10 Hz range eye oscillation is also rather variable within a trial compared with that of finger oscillation. Linking will obviously only occur during those trial sections where the eye oscillation is present and of a frequency matching the more regular finger oscillation.

(3) Some periods within experimental sessions may display quite strong and constant 10 Hz range coherence but this is sometimes greatly reduced when averaging of coherence is extended over a whole session. This is partly because the phase relationship between coherent oscillations is seen to vary over similar periods, as well as between different subjects and different trials, indicating a changing relative latency in transmission to the eyes and the finger. The result of this plasticity of latency is a cancelling of coherence when two periods having a different phase relation are averaged together over a whole session.

Slow *circa* 1 min variations in coherence between different central oscillations and between central oscillations and their peripheral manifestations have previously been described by Keidel *et al.* (1990). Other studies have indicated complex variations in phase relationships between 10 Hz range hippocampal oscillations (O'Keefe & Recce, 1993) and between the EMG oscillations of different postural muscles in primary orthostatic tremor (J. H. McAuley, T. C. Britton, J. C. Rothwell, L. J. Findley & C. D. Marsden, unpublished observations). However, in these studies the phase relationships appeared to be under some form of control and did not simply vary at random. The relatively long records required for reliable coherence analysis means that one is unable to explore the patterns of phase change in the present study. For example, it is possible that phase locking largely occurs only within each target sweep so that resumption of tracking after each change in direction introduces a 'jitter' between these short periods of temporary locking of two similar oscillations.

Conclusions

Common oscillations at around 3 and 10 Hz are shown to modulate the eye and limb movement systems. The 3 Hz linking of oscillations is likely to reflect shared visual feedback since it is dependent upon the existence of such feedback. On the other hand, the common 10 Hz oscillation is independent of visual feedback and could originate from a central motor oscillation that has a widespread influence across different control systems. The linking of 10 Hz oscillations displays plasticity and task specificity, suggesting a functional rather than anatomical basis and a possible role in hand–eye co-ordination.

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